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RESEARCH ARTICLE

Microclimate–forage growth linkages across two strongly contrasting precipitation years in a Mediterranean catchment

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Abstract

Given the complex topography of California rangelands, contrasting microclimates affect forage growth at catchment scales. However, documentation of microclimate–forage growth associations is limited, especially in Mediterranean regions experiencing pronounced climate change impacts. To better understand microclimate–forage growth linkages, we monitored forage productivity and root-zone soil temperature and moisture (0–15 and 15–30 cm) in 16 topographic positions in a 10-ha annual grassland catchment in California's Central Coast Range. Data were collected through two strongly contrasting growing seasons, a wet year (2016–17) with 287-mm precipitation and a dry year (2017–18) with 123-mm precipitation. Plant-available soil water storage (0–30 cm) was more than half full for most of the wet year; mean peak standing forage was 2790 kg ha⁻¹ (range: 1597–4570 kg ha⁻¹). The dry year had restricted plant-available water and mean peak standing forage was reduced to 970 kg ha⁻¹ (range: 462–1496 kg ha⁻¹). In the wet year, forage growth appeared energy limited (light and temperature): warmer sites produced more forage across a 3–4°C soil temperature gradient but late season growth was associated with moister sites spanning this energy gradient. In the dry year, the warmest topographic positions produced limited forage across a 10°C soil temperature gradient until late season rainfall in March. Linear models accounting for interactions between soil moisture and temperature explained about half of rapid, springtime forage growth variance. These findings reveal dynamic but clear microclimate–forage growth linkages in complex terrain, and thus, have implications for rangeland drought monitoring and dryland ecosystems modeling under climate change.

KEYWORDS

annual rangeland, climate change, forage growth, microclimate, soil moisture, soil temperature

1 | INTRODUCTION

Rangelands comprise the largest agricultural land-use class in California, covering about 23 million ha from deserts to open grasslands to oak savannahs (Fire Resource and Assessment Program, 2018). Forage from California's grasslands, which covers 5.6 million ha, provides 75%

of the annual forage for the California beef cow industry (Eviner, 2016), which was the state's fourth largest agricultural industry in 2017, grossing \$3.6 billion (California Department of Food and Agriculture, 2018). Rangelands also provide many ecosystem services including carbon storage, water supply, habitat for wildlife, aesthetic inspiration, and recreation and these may be susceptible to climate

change impacts (Byrd et al., 2015). California annual rangelands are typically found in the foothills between mountains and valley farmlands and along the coastal regions of California. Given their inherently complex topography, microclimates vary at short distances (10s of meters), as both air and soil temperatures have been documented to differ on north versus south aspects in California range improvement studies (Evans, Kay, & Young, 1975; Raguse & Evans, 1977). Terrain aspect, slope, hillslope position, and vegetation affect insolation and are the principal drivers of microclimatic differences (Geiger, Aron, & Todhunter, 2009). These differences extend into the soil mantle, affecting soil temperature, soil moisture, and plant growth. Moreover, differences in microclimate (including soil climate) across complex topography have been recognized as a force affecting ecohydrology and vegetation, which convey their effects on landscape evolution, for example, the steepening of north-facing slopes in the northern hemisphere midlatitudes (Poulos, Pierce, Flores, & Benner, 2012; Yetemen, Istanbuluoglu, Flores-Cervantes, Vivoni, & Bras, 2015; Pelletier et al., 2018). Thus, climate change implications for annual range production may vary considerably at the catchment scale and convey their effects on the future shape of the landscape.

Soil moisture is generally recognized as an important constraint on annual rangeland production given precipitation variability (e.g., amount and seasonal distribution) in California's Mediterranean climate (Becchetti et al., 2016a). Several studies have developed linear regression models describing relationships among site precipitation, air temperature, and peak annual forage growth across diverse California climates (Duncan & Woodmansee, 1975; George et al., 1988; George, Williams, McDougald, Clawson, & Murphy, 1989; Murphy, 1970; Pitt & Heady, 1978). These studies showed that higher productivity is associated with higher rainfall but the relationship is not simple. Productivity depends on the timing of precipitation and coincidence of available moisture with suitable temperatures and light availability. Together, these factors are recognized to control California annual range growth across four distinct growth phases: (1) fall or winter germination following at least 1.25–2.5 cm precipitation in less than a week with rapid fall growth if the temperature is in the ideal range of 16–27°C; (2) slow winter growth if the temperature is <10°C and little growth if the temperature is <5°C, pending available moisture and light; (3) rapid growth with spring warming and longer days, pending available soil moisture; and (4) peak forage from early April to end of May, depending on region and weather, but generally as a result of exhausting root-zone soil moisture (0–30 cm for annual species, George et al., 1988; Becchetti et al., 2016a). Thus, average production can occur in both relatively high and low rainfall years, as recently documented at 26 range-monitoring sites across California (George et al., 2010).

Forage production in California rangelands is highly variable between years (George et al., 2010) because of the vagaries of atmospheric rivers that provide the majority of annual precipitation in California (Swain, Langenbrunner, Neelin, & Hall, 2018). This makes cattle production in California a risky enterprise because livestock herd numbers and movements are difficult to optimize or to adapt quickly (Shrum, Travis, Williams, & Lih, 2018). Improvements in predicting

range forage production could help range managers adjust stocking rates to match available forage and leave sufficient residual dry matter for sustainable regeneration of California's annual grasslands (Bartolome, Frost, & McDougald, 2006). Additionally, these predictions could be used to better understand possible climate change impacts on range production, informing long-term land planning by the livestock industry and local land management agencies. Climate change is expected to negatively impact southwestern US rangeland production (Reeves, Bagne, & Tanaka, 2017; Reeves, Moreno, Bagne, & Running, 2014), including most of California (Shaw et al., 2011). However, model projections for San Francisco Bay Area rangelands indicated that climate change could bring increased productivity but a shorter growing season (Chaplin-Kramer & George, 2013). Forecasting climate change impacts on California rangelands is inherently difficult given the uncertainty of the global emissions trajectory and the possibility for species distribution shifts (Thorne et al., 2017). Shifting weather patterns with climate change are likely to have differential effects across California's diverse topography. While several California rangeland studies document differences in microclimate, species composition, and growth rate on north versus south aspects (Evans et al., 1975; Hufstadler, 1978; Raguse & Evans, 1977) or study topography-related differences in soil moisture at catchment scale (Beaudette, Dahlgren, & O'Geen, 2013), no studies have simultaneously investigated forage growth and soil moisture and temperature in the root zone of California's annual range where precipitation is more limited. Moreover, coupled range productivity and meteorology monitoring have only occurred since 2003 in the more precipitation-limited climates of California, such as eastern San Luis Obispo County (Larsen, Striby, & Horney, 2014). It is these drier rangelands that are expected to be most vulnerable to future changes in climate, especially to more extreme variations in precipitation.

We studied associations among soil moisture, soil temperature, topography, and forage production in a 10-ha catchment through two contrasting growing seasons, a wet growing season (2016–17; 287 mm) that officially ended an extreme drought (AghaKouchak, Cheng, Mazdiasni, & Farahmand, 2014), followed by another dry growing season (2017–18; 123 mm), a pattern not atypical of the site's interannual precipitation dynamics (Figures S1–S2). The study objective was to improve understanding of how topographic and microclimatic complexity in California's semi-arid rangelands is related to catchment-scale temporal and spatial variability in forage growth. Specifically, we attempt to answer the following three questions: (1) To what extent does forage growth vary at the catchment scale across two contrasting growing seasons (wet versus dry)? (2) To what extent are catchment-scale differences in soil moisture and soil temperature (microclimate) apparent across these contrasting growing seasons? and (3) To what extent are catchment-scale differences in microclimate linked to spatial and temporal patterns in forage growth? Results of this study will inform topographic relationships to forage growth at the catchment scale and eventually provide validation for high-resolution, regional climate change modeling using earth system models (Huang, Rhoades, Ullrich, & Zarzycki, 2016).

2 | METHODS

2.1 | Study site description

The study site was located in an annual grassland with no trees or shrubs on a private ranch in the eastern foothills of California's Central Coast Range. Annual peak standing forage has been monitored since 2001 within the 10-ha catchment with elevation ranging from 467 to 508 m (Larsen et al., 2014). The catchment is in eastern San Luis Obispo County, 56 km inland from the Pacific Ocean. It is located in the lowest precipitation zone of the county in the rain shadow of Coast Range peaks (Figure 1). The study site's Mediterranean climate consists of cool winters (mean 1980–2010 January temperature = 7.9°C) with sporadic precipitation that occurs mostly from October to May (mean annual precipitation = 334 mm), along with extended dry, hot summers (mean July temperature = 23.5°C, Daly et al., 2008). Measured precipitation was 53%–54% less than that estimated by PRISM in both study years, that is, the recorded precipitation measured 246 mm and 104 mm less during the 2016–17 and 2017–2018 growing seasons, respectively (Figure S1). Large growing season swings in precipitation are common in the historical record (Figure S2). Forage documented in 2016–17 included the following nine annual species, listed in order of prevalence: *Bromus madritensis* (red brome); *Erodium cicutarium* (filaree); *Festuca microstachys* (annual fescue); *Acmispon*

wrangelianus (California clover); *Avena occidentalis* (wild oats); *Astragalus didymocarpus* (two-seeded milkvetch); *Centaurea melitensis* (tocalote); *Lipidium* sp. (mustard); and *Amsinckia menziesii* (fiddleneck, Figure S3). Fourteen years (2001–2014) of forage monitoring at the site showed an average of 1,665 kg ha⁻¹ peak standing dry biomass, ranging from 132 kg ha⁻¹ in 2014 to 4,205 kg ha⁻¹ in 2011 (Becchetti et al., 2016b).

The study site was selected as an example of complex topography in California annual rangelands, including summit, shoulder, backslope, footslope, and concave–linear–convex surface curvatures with slopes ranging from 0 to 20° (Figure 1). Of the total catchment area, 45% was south facing, 29% was west facing, 24% was north facing, and 2% was east facing (Liu et al., 2019). Soils formed from a mélange of sedimentary bedrock and colluvium ranging from sandstone to shale. One soil map unit (Balcom-Nacimiento complex on 15%–30% slopes) is mapped at the study site with two major soil components occurring on backslope positions: Balcom (45% of map unit), an Inceptisol in the fine-loamy, mixed, superactive, thermic Typic Calcixerepts family, having a coarse sandy loam ecological site description (ID: R015XF031CA); and Nacimiento (30% of map unit), a Mollisol in the fine-loamy, mixed, superactive, thermic Calcic Haploxerolls family, having a fine-loamy ecological site description (ID: R015XE020CA, Soil Survey Staff, 2003). These two soils are distinguished by A horizon thickness and depth to a Bk horizon. The remaining 25% of the map

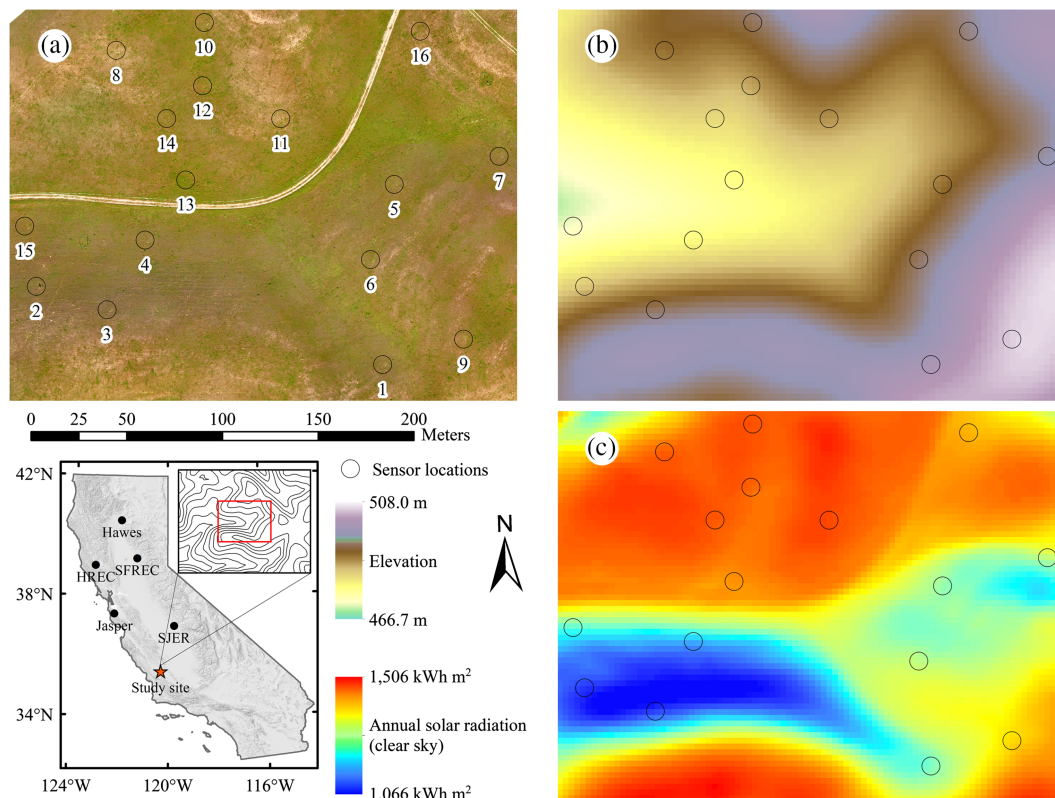


FIGURE 1 Annual rangeland study catchment (10 ha) in the eastern foothills of California's Central Coast Range: (a) RGB image, (b) elevation, and (c) annual solar radiation, with locations of sensors shown as circles. The locations of several long-term California range monitoring and research sites referred to in the text are also highlighted on the inset map: San Joaquin Experimental Range (SJER); Hopland Research and Extension Center (HREC); Sierra Foothill Research Center (SFREC); Jasper Ridge (Jasper); and Hawes Ranch (Hawes).

unit is an assortment of 12 minor soil components, mostly found on other hillslope positions (e.g., summit and footslope). Pedogenic calcium carbonate was observed throughout the site and generally increased with depth; it appeared to be nearer to the surface at summit and shoulder hillslope positions.

2.2 | Instrumentation

Sixteen locations were chosen within the 10-ha catchment to monitor soil moisture, soil temperature, and forage growth using expert opinion and a random-stratified design commonly used in catchment studies (de Groot, Brus, Bierkens, & Kotters, 2006; Beaudette et al., 2013; Figure 1). The number of landscape components in each part of the catchment reflected its approximate relative proportion by area. A minimum distance of 25 m was required between locations within stratified hillslopes, using the Create Random Points tool in the ArcGIS Desktop 10.5 software.

To monitor soil moisture and temperature in the annual grass root zone, we installed 64 Decagon Devices 5TM sensors across the study area on November 16–18, 2016, at two depths (7 and 22 cm) with duplicates at each depth per location (four sensors per location). Because sensors are influenced by moisture content up to 6 cm away from the center of the sensor (Meter Group, 2018), data from the 7-cm depth are referred to as the 0–15 cm depth and data from the 22-cm depth are referred to as the 15–30 cm depth. At each location, two subsampling locations were randomly chosen within a 1-m quadrat, while requiring a minimum 40-cm separation between subsample locations. At each subsampling location, a 30-cm deep by 10-cm diameter hole was dug and a sensor was inserted horizontally at each depth into the upslope pit face. Excavated soil was placed on tarps and backfilled into the hole in the same order it was removed to achieve a similar bulk density to the undisturbed soil. Decagon Em50 data loggers recorded soil temperature and volumetric soil moisture every 15 min using the factory default calibration curve for soil moisture. Data loggers were removed and sensor cables buried on July 20, 2017, to allow for grazing of dry residual forage by a cow–calf herd managed on the ranch. Other than this grazing period, cattle were excluded by a temporary electric fence surrounding the catchment. Data loggers were reinstalled on November 28, 2017, before precipitation began in the second growing season. Precipitation was measured with three tipping bucket rain gauges within the catchment and averaged by day.

2.3 | Monitoring forage growth

To monitor forage growth, we clipped standing forage at four dates during each growing season, spaced approximately one month apart. For each date and location, two subsamples, each covering a 30-cm quadrat, were clipped 1.5 m away from the center of the soil sensors to avoid trampling forage above the sensors (32 total samples per date and averaged by location). Sampling locations were selected at an opposite, randomly assigned angle from the center of the sensors. Clipped forage was oven dried at 60°C for 48 hr before weighing.

We also measured the grass height and recorded the species composition using the simplified ranking method (Ratcliff & Frost, 1990) for each subsample in the 2016–17 growing season (Figure S3).

2.4 | Catchment terrain characteristics

Terrain characteristics were derived using the ArcGIS Desktop 10.5 software from a 1.86-cm per pixel digital surface model of the study area, which was created using photogrammetric imagery captured by a drone on March 9, 2017 (Table S1, Liu et al., 2019). Seven ground control locations showed a mean RMSE of 6 cm (all dimensions). High resolution data were aggregated to 30 cm (ArcGIS: Spatial Analyst: Generalization: Aggregate) and then filtered to smooth anomalies using the default low-pass option (ArcGIS: Spatial Analyst: Neighborhood: Filter). Data were then aggregated to 3 m and filtered again before calculating elevation, slope, aspect, curvature (profile, plan, and mean), and annual clear sky solar radiation (insolation) using the ArcGIS Spatial Analyst tools. The filtering process was necessary to produce stable estimates of terrain curvature. A second digital surface model produced from November 2016 drone imagery was used as a quality control check on terrain characteristic estimates for the sixteen locations, showing $R^2 > 0.99$ for comparisons of elevation, slope, insolation, and aspect and $R^2 = 0.94$ – 0.97 for curvature.

2.5 | Aggregation of soil moisture and temperature data and statistical analysis

The monitoring approach and instrumentation were designed to analyze data using regression and rank correlation to understand associations between microclimate and forage growth. Fifteen-minute interval soil temperature and moisture data were averaged by day and each sensor ($n = 64$) after confirming that there were no anomalous values. Five sensors were completely removed from the analysis because of malfunctions but all sixteen locations had at least one working sensor per depth. Aggregated daily sensor data were then averaged by location and depth to produce 32 daily average soil moisture and temperature records through each growing season, one for 0–15 cm and one for 15–30 cm at each location. In 2017, a data logger malfunctioned at Location 13 (Figure 1), so reliable data were missing from 3/10 to 4/25 for all variables and depths at this location. Missing temperature and volumetric water content (VWC) data were gap-filled at five sensors which had been accidentally disconnected for 4–22 days from 1/29/2018 to 2/19/2018. Specifically, for VWC, daily values were assumed to decrease linearly from the last reading before disconnection to first reading after reconnection, because this was a rain-free period. For soil temperature, gap-filling was accomplished by exploiting a $R^2 > 0.99$ linear relationship with nearby sensors to estimate the more dynamic, missing temperature data for the unplugged sensors.

Soil moisture data were transformed to an index of plant-available water, where a value of 1 represents field capacity and 0 represents wilting point, based on information from the soil moisture hydrographs during the wettest and driest periods of 2017. For the

0–15 cm sensors, field capacity was taken as the average of Jan 17 and Jan 27, 2017 VWC by location. Both of these dates were 4 days after multiday saturating precipitation events ended. For the 15–30 cm sensors, field capacity was taken as the average of Jan 18 and Jan 28, 2017 VWC by location, which is when average daily change in VWC across 15–30 cm sensors was similar to those at 0–15 cm (-0.003 VWC day $^{-1}$). To approximate wilting point by location, soil moisture contents at 0–15 cm were assumed to be air-dry at the end of a 7-month dry period (December 2017), averaging 9% across locations. Wilting point was assumed to be twice these “air-dry” moisture contents, a common assumption to estimate total evaporable water in soil surface evaporation research (Allen, Pereira, Smith, Raes, & Wright, 2005). This resulted in an assumed average wilting point of 18% from 0 to 15 cm across all locations. At 15–30 cm, drying was not as intensive after 7 months, averaging 13%. Given the similar soil textures between the 0–15 cm and 15–30 cm layers, we assumed that the average wilting point at 15–30 cm was also 18% across all sixteen locations.

We used Pearson correlation tests to examine associations between relative soil moisture depletion and temperature and also to explore daily associations between each of these variables and forage growth variability across the catchment. Both simple and multiple least-square regression models that also considered an interaction between relative soil moisture depletion and temperature were used to test associations between microclimate and both standing forage and forage growth between clipping dates. For these tests, relative soil moisture depletion and temperature were averaged by location for the specified time period, for example, growth from mid-March to mid-April was compared with average soil moisture and temperature during the same time period. Finally, spatial autocorrelation in microclimate and forage data was examined by calculating daily Moran's I through a Monte-Carlo approach in the R software (R Core Team, 2016). Daily p values were estimated by the *moran.mc* function from the *spdep* package (Bivand & Wong, 2018) with 999 random permutations for each day's data, whereby daily data were randomly reassigned to one of the locations and Moran's I was recalculated. The p values reflect a ranking of the actual observed Moran's I relative to the random permutation, and is thus, an approximate probability that the day's spatial autocorrelation was produced by chance alone.

TABLE 1 Pearson correlation coefficients between standing forage at different dates and four different terrain characteristics derived from a 3-m resolution DEM

Sampling date	Elevation	Annual radiation	Slope	Mean curvature
2/15/2017	-0.42	0.42	-0.34	-0.50
3/14/2017	-0.33	0.58	-0.59	-0.27
4/10/2017	-0.44	0.05	-0.09	-0.33
5/1/2017	-0.47	-0.02	-0.32	-0.47
2/15/2018	-0.19	0.07	0.04	-0.63
3/22/2018	-0.07	-0.47	0.05	-0.22
4/15/2018	0.26	0.17	-0.58	-0.13

Note. Significant results ($\alpha = 0.05$) are shown in bold. Notable results ($\alpha = 0.1$) are shown in italics. Sample size = 16.

3 | RESULTS

3.1 | Terrain characteristics and association with forage growth

The sixteen study locations within the 10-ha catchment captured a range of terrain features across a 30-m elevation span of different hill-slope positions and complex topography. Six monitoring sites were south facing, five were north facing, and five were west facing with annual clear sky insolation ranging from 1,102 to 1,471 kWh m $^{-2}$. Slopes ranged from 5.6° to 21.8° and positions covered examples of convex, linear, and concave mean curvatures (Figure 1; Table S1).

Various terrain characteristics were associated with variability in standing forage but the associations themselves were variable within growing seasons and across the two contrasting growing seasons (2016–17, referred to as the wet year, and 2017–18, referred to as the dry year). In both years, concave sites (generally negative mean curvature) were significantly associated with higher standing biomass early in the season in February (Table 1). In March, standing forage showed the strongest association to terrain aspect and slope. In the wet year, south-facing, gentler slopes showed accelerated forage production; in the dry year, the relationship reversed with locations receiving higher energy showing notably lower production during a midwinter drought with only marginal recovery in early April 2018 (Figure 2; Table 1). Dry year peak standing forage in April 2018 was also significantly reduced on steeper slopes (Table 1). At peak standing biomass in the wet year (April 2017), lower elevation and concave sites tended to have more standing forage but relationships were statistically nonsignificant (Table 1).

3.2 | Forage production in a wet and dry year

Comparing the wet and dry years, mean standing forage was consistently 3-times greater throughout the growing season from early (February) to peak standing forage (April) in the wet year (Figure 2). Peak standing forage was $2,790 \pm 940$ kg ha $^{-1}$ in the wet year (mean \pm sd) across the catchment and 970 ± 350 kg ha $^{-1}$ in the dry year. While coefficients of variation in forage production were similar across the months and two years at 0.4–0.5 (Table S2), the range in peak standing

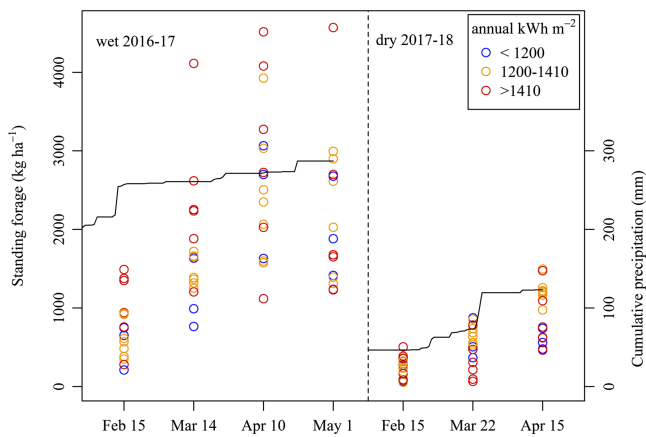


FIGURE 2 Standing forage and cumulative precipitation across two contrasting growing seasons. Each point is an average of two clippings per time period at the location. Cumulative precipitation records begin on October 1 and are shown from February 5 through the last clipping date for each growing season. Point symbols are displayed in three different classes based on annual clear sky solar radiation (insolation) for the location in the catchment. Red is south facing and southwest facing, orange is west facing and northwest facing, and blue is north facing.

forage was nearly $3,000 \text{ kg ha}^{-1}$ in the wet year, 2.9-times the range and 2-times the maximum standing forage observed in the dry year. Thus, in terms of absolute forage biomass, spatial variability in the wet year was much greater.

While growing season precipitation was 2.3-times higher in the wet year (287 vs. 123 mm), early season production in the wet year was enabled by fall precipitation that continued through the winter until a dry spell in late February and March 2017 (Figure S1). In the dry year, germinating rains did not occur until January and were immediately followed by a dry period lasting until late March. During the dry year, 60% of the precipitation fell late in the growing season in March and April, whereas March was relatively dry in the wet year.

3.3 | Soil moisture and temperature (microclimate) associations with forage growth across years

From a plant-available water perspective, there were several remarkable differences between the two years linked to the three-fold difference in forage production between growing seasons. In the wet year, on average, the 0–15 cm soil layer remained above 50% plant-available water storage for 80% of the period between December 1 and April 15 (Figures 3; S4). In the dry year, the 0–15 cm layer remained above 50% plant-available water for 29% of the same period (Figures 3, S4). Deeper in the root zone, the comparison was even starker. In the wet year, the 15–30 cm layer remained above 50% plant-available water storage for 64% of this period and all locations were clearly above wilting point from January 10 through peak standing biomass (Figures 4; S4). In the dry year, the 15–30 cm layer only remained above 50% plant-available water storage for 11% of this period (Figures 4; S4). Rains were not sufficient until late March to recharge the entire root zone (Figures 3, 4).

There were clear linkages between soil moisture and temperature but these associations were dynamic. Consistent differences in soil temperature across the two years were observed as a function of annual clear sky insolation (Figures 5, 6). However, variability in soil temperature depended on soil moisture status. For instance, mean 0–15 cm soil temperatures for the January 10–April 15 period were 12.5°C (range $10.5\text{--}14.1^{\circ}\text{C}$) in the wet year and 14.3°C (range $10.6\text{--}17.0^{\circ}\text{C}$) in the dry year (Figure 5). When moisture became severely limited in late February 2018, the range in 0–15 cm soil temperatures across the catchment averaged 10.2°C for 10 days, compared with a range of 3.1°C during the January–February 2017 wet period (Figures 5, 6). Also linked to warmer soils was enhanced soil moisture drawdown at times, for instance, very clearly in late November through December 2016 (Figures 3, 4, 7). Up to 80% of daily differences in plant-available water in the 30-cm root zone could be explained by differences in soil temperature during this wetting-up

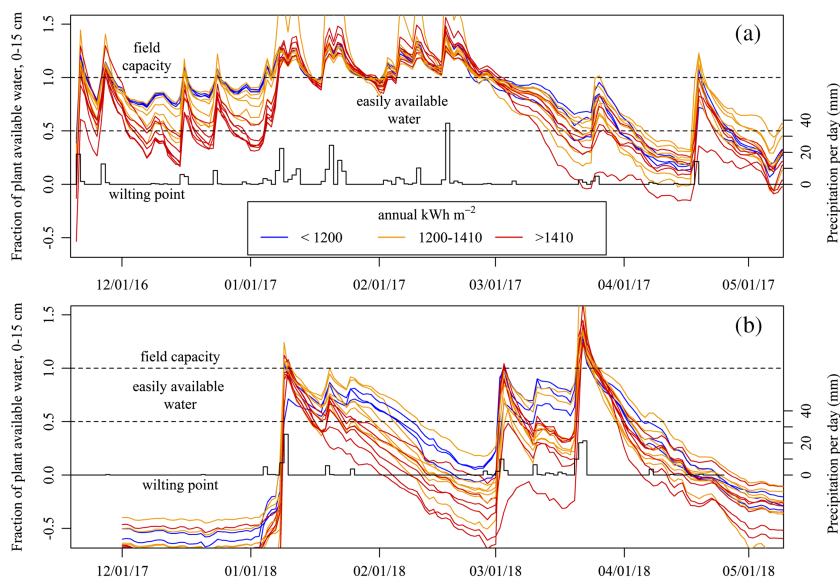


FIGURE 3 a–b: Soil moisture availability in the 0–15 cm layer across all 16 monitoring locations where (a) is the 2016–17 growing season and (b) is the 2017–18 growing season. Lines are symbolized by annual clear sky insolation where red is south facing to southwest facing, orange is west facing to northwest facing, and blue is north facing.

FIGURE 4 a–b: Soil moisture availability in the 15–30 cm layer across all 16 monitoring locations where (a) is the 2016–17 growing season and (b) is the 2017–18 growing season. Lines are symbolized by annual clear sky insolation where red is south facing to southwest facing, orange is west facing to northwest facing, and blue is north facing.

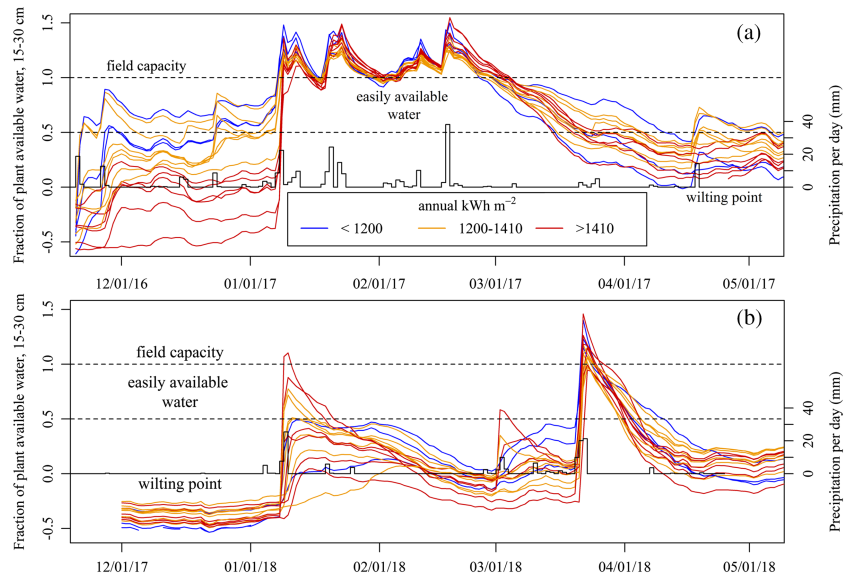
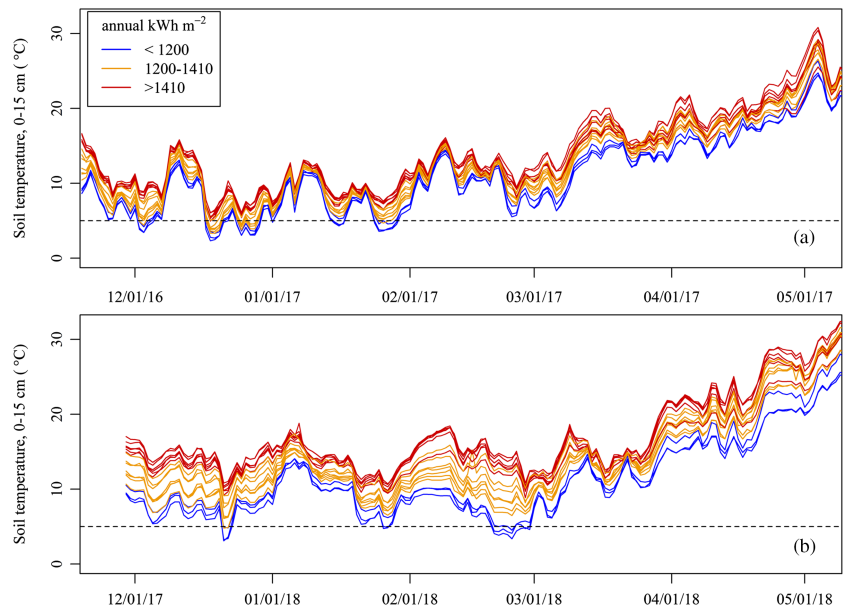


FIGURE 5 a–b: Soil temperature in the 0–15 cm layer across all 16 monitoring locations where (a) is the 2016–17 growing season and (b) is the 2017–18 growing season. Lines are symbolized by annual clear sky insolation where red is south- to southwest-facing, orange is west- to northwest-facing, and blue is north-facing. Dashed horizontal line is 5°C, the base temperature at which cool-season annual species, such as in California annual range, typically cease growth (George et al. 1988).



period, before heavy rains in January 2017 (Figure 7). In the dry year, there was no evidence of an aspect effect on soil moisture drawdown until the first appreciable rainfall in January 2018 (Figures 3, 4, 7).

There were also clear linkages between soil temperature and moisture (microclimate) and forage growth. While the warmest sites may have experienced some moisture stress during the November–December 2016 wetting-up period, since soil moisture fell below 50% plant-available water storage, this did not appear to negatively impact early-season forage growth on south-facing slopes measured in February 2017 (Figure 2; Table 1). Warmer soil temperatures were clearly linked to more rapid, springtime forage growth in the wet year (Figures 8a & c). The same association between warmer soil temperatures and soil moisture drawdown was evident in late February and early March 2017 as soils dried down but the relationship was not as strong (Figures 3, 4, 7). By mid-March 2017, this soil moisture–temperature

association had completely dissipated, suggesting biological controls on soil moisture drawdown (transpiration, Figures 3, 4, 7–8d) or lateral soil moisture transport to lower landscape positions, subsidizing these more productive locations (Table 1). Nearly half of mid-March to mid-April 2017 growth could be explained by differences in soil moisture availability across locations (Figure 8d). Thus, by peak standing forage in April 2017, the energy limitation on forage growth was no longer evident (Figure 8b) but growth was favored in concave and low elevation locations across all terrain aspects (Table 1; Figure S5).

A markedly different scenario emerged in the dry year in regard to the microclimate–forage linkages. Soils dried well below wilting point to at least 30-cm depth through the hot, dry summer in spite of ample residual dry matter left by a late fall grazing of the study site. Precipitation in early January 2018 triggered germination and shallow soil moisture levels were above 50% plant-available water for several

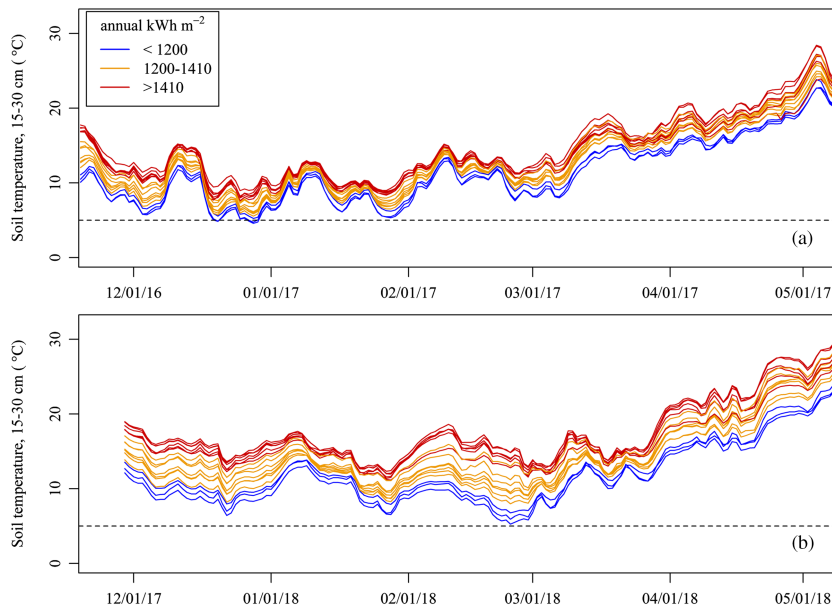


FIGURE 6 a–b: Soil temperature in the 15–30 cm layer across all 16 monitoring locations where (a) is the 2016–17 growing season and (b) is the 2017–18 growing season. Lines are symbolized by annual clear sky insolation where red is south- to southwest-facing, orange is west- to northwest-facing, and blue is north-facing. Dashed horizontal line is 5°C, the base temperature at which cool-season annual species, such as in California annual range, typically cease growth (George et al. 1988).

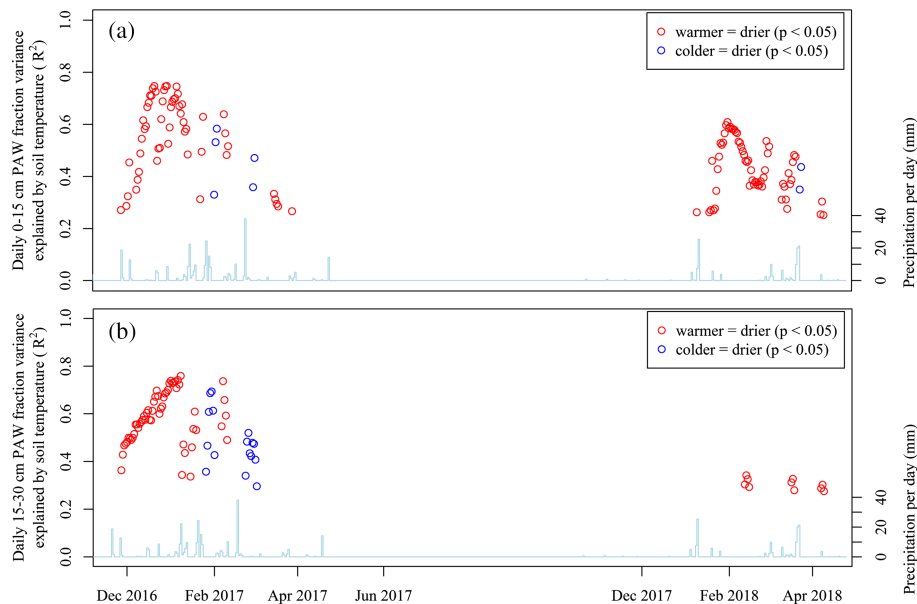


FIGURE 7 a–b: Fraction of total plant-available water (PAW fraction) variance explained by soil temperature when the relationship was statistically significant ($\alpha = 0.05$) at (a) 0–15 cm and (b) 15–30 cm. Color of symbols indicates the sign of the relationship.

weeks (Figures 3, 4). However, lack of precipitation led to soil moisture levels near wilting point by early February 2018 across the catchment. A combination of low soil moisture availability and warm soil temperatures was associated with a decline in standing forage on most south-facing locations until late March 2018 when rains returned (Figure 9). Warmer sites tended to be drier through this midwinter drought (Figures 3, 4, 7) but forage growth was similarly low across microclimates except for the warmest sites, suggesting an interaction between temperature and moisture that was confirmed with a linear model accounting for this interaction (Figures 9, 10; Table 2). When

rains returned in late March and early April 2018, soil moisture was no longer limiting in the 30-cm root zone across all sites (Figures 3, 4). On cue, the relationship between soil temperature and forage growth completely changed in the last 20 days of the dry year and warmer sites were once again more productive (Figures 9, 10; Table 2). These contrasting growth periods produced a nonlinear relationship between microclimate and peak standing forage in mid-April 2018 (Figure 9a–b). All of the northwest- to west-facing slopes outperformed the north- and south-facing sites in the dry year (Figure S5).

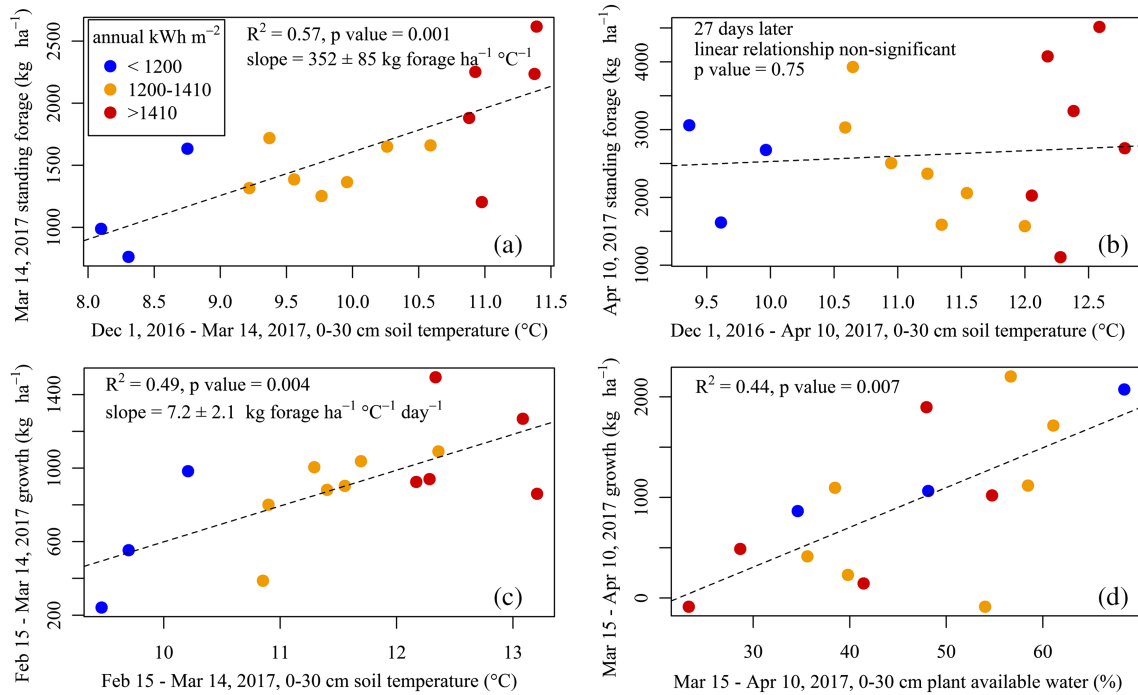


FIGURE 8 a–d: Wet growing season (2016–17) relationships between 0–30 cm mean soil temperature (x-axis) and (a) standing forage in mid-March, (b) standing forage 27 days later in mid-April (c) forage growth from mid-February to mid-March 2017, and (d) relationship between fraction of total plant-available water in the 0–30 cm root zone (x-axis) and forage growth from mid-March to mid-April 2017. Points are colored by annual clear sky insolation (kWh m^{-2}). A high leverage outlier (location 13) was removed from Figure 8a and 8c based on Cook's distance > 1 and from Figure 8d because of missing soil moisture data that could not be reliably gap-filled.

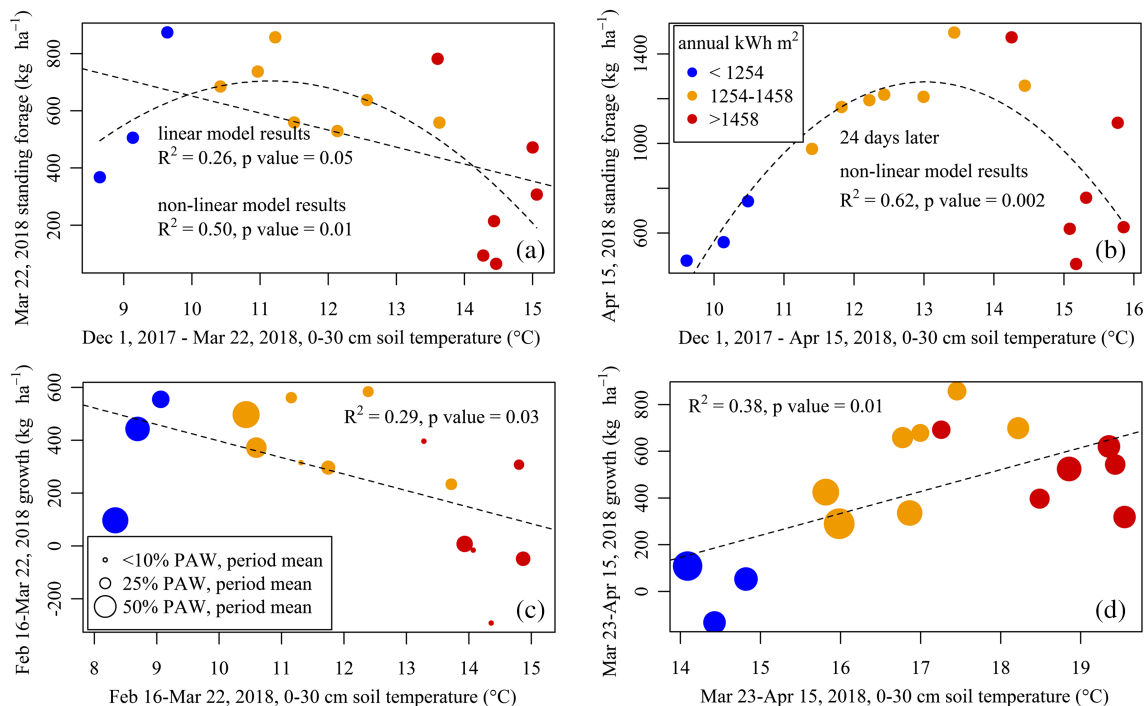


FIGURE 9 a–d: Dry growing season (2017–18) relationship between 0–30 cm root-zone soil temperature (x-axis) and (a) standing forage in mid-March, (b) standing forage 24 days later in mid-April, (c) forage growth from mid-February to mid-March 2018, and (d) forage growth from mid-March to mid-April 2018. All points are colored by annual clear sky insolation (kWh m^{-2}). Symbol size in (c) and (d) are drawn according to average percent of total plant-available water (PAW) in the 0–30 cm root zone at the location

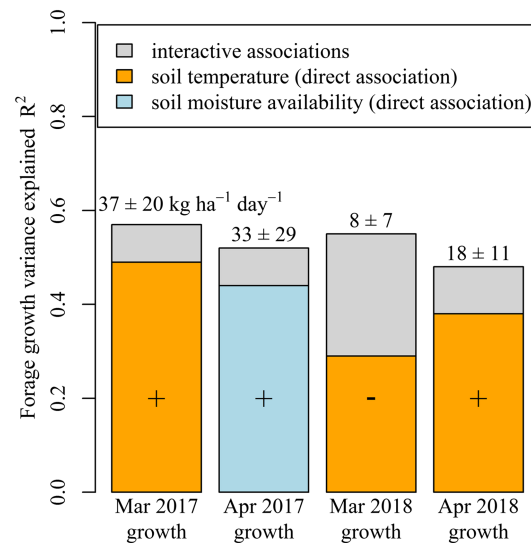


FIGURE 10 Microclimate association with forage growth varied through two growing seasons and consistently explained about half the variability in forage growth. Significant ($\alpha = 0.05$) positive (+) and negative associations (–) with either soil temperature or soil moisture availability (fraction of plant-available water) indicated on bars. Significant interaction occurred only during March 2018 growth ($p = 0.04$). Mean \pm sd forage growth rates are noted above each bar

TABLE 2 Soil moisture and temperature (0–30 cm) associations with rapid, springtime forage growth during the wet 2016–17 and dry 2017–18 growing seasons, as derived from linear regression models

Period	Model	R^2	AIC	LOOCV	Overall	Model	SM	T	SM * MT	SM	T	SM * T
						p values				Parameter slopes ($\text{kg ha}^{-1} \text{sd}^{-1}$)		
Mar 2017 growth	SM	0.03	219.7	366	323	0.566	0.566	NA	NA	51	NA	NA
	T	0.49	210.1	260	234	0.004	NA	0.004	NA	NA	220	NA
	SM + T	0.49	212.0	293	243	0.017	0.742	0.006	NA	22	217	NA
	SM * T	0.57	211.5	347	233	0.022	0.470	0.008	0.185	49	204	88
Apr 2017 growth	SM	0.44	238.0	614	593	0.007	0.007	NA	NA	509	NA	NA
	T	0.23	242.8	738	696	0.068	NA	0.068	NA	NA	–370	NA
	SM + T	0.50	238.4	615	585	0.016	0.026	0.262	NA	430	–200	NA
	SM * T	0.52	239.7	662	598	0.038	0.033	0.309	0.500	425	–187	–102
Mar 2018 growth	SM	0.02	227.4	280	262	0.647	0.647	NA	NA	32	NA	NA
	T	0.29	222.2	245	222	0.031	NA	0.031	NA	NA	–138	NA
	SM + T	0.34	222.9	261	222	0.065	0.332	0.024	NA	–70	–178	NA
	SM * T	0.55	219.1	216	192	0.020	0.148	0.003	0.040	–95	–256	135
Apr 2018 growth	SM	0.31	223.8	241	233	0.026	0.026	NA	NA	–150	NA	NA
	T	0.38	222.0	236	221	0.011	NA	0.011	NA	NA	167	NA
	SM + T	0.47	221.3	238	211	0.015	0.152	0.062	NA	–93	125	NA
	SM * T	0.48	223.2	250	218	0.043	0.174	0.068	0.717	–108	129	–33

Note. When the model was significant ($\alpha = 0.05$), significant parameters are shown in bold. Soil moisture and temperature were averaged by location ($n = 16$) and both depths (0–15 and 15–30 cm) for each growth period and normalized to calculate standardized parameter estimates.

SM = normalized soil moisture availability, using relative index of plant-available water (see Methods 2.5); T = normalized soil temperature; SM + T = normalized soil moisture availability and temperature; SM * T = normalized soil moisture availability and temperature with interaction. AIC = Akaike information criterion; LOOCV = leave-one out cross validation of model; RMSE = root mean square error; sd = standard deviation.

3.4 | Spatial autocorrelation of soil temperature, moisture, and forage growth

Testing spatial autocorrelation in soil temperature, moisture, and forage growth supported the finding of variable microclimate–forage growth linkages. The spatial autocorrelation in soil moisture and forage

production was found to vary at different times of the year through both wet and dry years. In contrast, soil temperature demonstrated very strong autocorrelation during nearly 100% of both growing seasons (Table 3; Figures 5, 6). Relative depletion of plant-available soil moisture showed significant ($\alpha = 0.05$) spatial autocorrelation for 34%–50% of the growing season, depending on the year and depth, except for the

TABLE 3 Proportion of each growing season (Dec 1–May 1) with significant ($\alpha = 0.05$) spatial autocorrelation for the 16 monitored microclimates, including soil temperature, soil volumetric water content (VWC) and soil moisture transformed to a fraction of plant-available water (PAW index) at both 0–15 and 15–30 cm depths (see Methods 2.5)

Depth	Microclimate feature	Fraction of growing season (%) with significant autocorrelation	
		2016–17 (wet year)	2017–18 (dry year)
0–15 cm	Soil temperature	99%	100%
	VWC	6%	19%
	PAW index	34%	36%
15–30 cm	Soil temperature	100%	100%
	VWC	14%	0%
	PAW index	49%	1%

15–30 cm layer in 2018, where wetting did not consistently occur until late March (Figure 4). Absolute volumetric soil moisture values demonstrated spatial autocorrelation less than 20% of each growing season at both depths (Table 3). Variability in forage production was greater in the wet year, and this was reflected in the lack of spatial autocorrelation in forage production at peak standing forage in April 2017 due to a late season growth spurt at moister sites that nullified the previous month's aspect association (Table 4; Figure 8d). In contrast, forage production was highly spatially correlated at peak production in the dry year, further supporting the soil temperature and aspect linkages to forage growth in the dry year (Tables 2, 4; Figure 9).

4 | DISCUSSION

4.1 | Forage growth across years and linkages to microclimate

Forage growth was not uniform across the grassland catchment with 0.4–0.5 coefficients of variation through all sampling dates (Table S2). In a wet-year, the range in forage production exceeded the maximum standing forage observed in a dry year (Figure 2; Table S2). This level of spatial variability in a single catchment rivals interannual variability documented at four multidecadal rangeland monitoring sites in California: San Joaquin Experimental Range (SJER: CV = 0.365 and

TABLE 4 Evidence for non-random spatial patterns in standing forage and monthly forage growth in the catchment

Year	Day	Standing forage	Past month's growth
		---autocorr. <i>p</i> values---	
2017	Feb 15	0.093	NA
	Mar 14	0.036	0.045
	Apr 10	0.622	0.403
2018	Feb 15	0.951	NA
	Mar 22	0.044	0.019
	Apr 15	0.039	0.015

Note. *p* values reflect approximate probability that observed spatial autocorrelation (autocorr.) could be because of chance alone (see Methods).

$n = 79$); Hopland Research and Extension Center (HREC: CV = 0.249 and $n = 61$); Sierra Foothill Research Center (SFREC: CV = 0.309 and $n = 31$); and Hawes Ranch (CV = 0.425 and $n = 41$; Figure 1; Becchetti et al., 2016b).

Microclimatic differences were relatively large across the catchment and associated with forage growth variance in a dynamic fashion. Differences of up to 10°C in shallow soil temperatures during dry periods were observed (Figures 5, 6). Differences in plant-available soil moisture related to differences in insolation and soil temperature were also observed, most clearly at the beginning of each growing season after the first rainfall events (Figures 3, 4, 7). Differences in root-zone soil moisture and temperature at the scale of 10s of meters explained half the variability in forage growth rates across the catchment (Figures 8–10; Table 2). But the specific growth rate association to microclimate varied through each growing season (October–April) and by year. For example, we observed distinct moist periods when warmer landscape positions were linked to faster forage growth rates, a dry period in a wet year when growth was faster in moister soils that spanned the temperature gradient, and a midwinter drought in a dry year when forage growth suffered on the warmest sites where soils had dried to near wilting point or less (Figures 8–10; Table 2). The large degree of microclimate variability at the catchment scale in this annual grassland with no tree cover demonstrates the usefulness of understanding microclimate associations to forage growth in different regions and vegetation types of California rangelands, because these associations may be diverse and impacted by climate change.

Several recent studies have observed remarkable variability in soil temperature in complex topography at relatively small scales that can exceed the adiabatic lapse rate, such as mountainous, alpine terrain in central Norway (Wundram, Pape, & Löffler, 2010), nested grassland catchments in New South Wales, Australia (Kunkel, Wells, & Hancock, 2016), and a forested mountain watershed in Montana (Liang, Riveros-Iregui, Emanuel, & McGlynn, 2014). Studies of California annual rangelands have documented aspect-related differences in soil temperature/moisture and forage growth. Evans et al. (1975) studied soil moisture, temperature, and forage growth and composition in the context of an herbicide treatment on both north and south slopes at the wetter SFREC site (750 mm precipitation yr^{-1}). Like our study, they observed greater moisture depletion on south-facing slopes during dry, midgrowing season periods and also 2–10°C warmer temperatures on south compared with north slopes. During the wettest year, they observed enhanced forage growth on south-facing slopes, consistent with our study site's behavior when soil moisture was plentiful. Another study of southern California rangeland found that species on south-facing slopes completed their life cycles up to a month more rapidly than on north-facing slopes and reached higher growth rates during wet periods (Hufstader, 1978). In contrast, a one-year study of aspect associations with forage growth and composition across contrasting parent materials at Jasper Ridge found decreasing productivity from north to south aspects on sandstone but no differences in forage production between aspects on serpentine-derived soils (McNaughton, 1968).

During our study's first growing season (wet year), temperature was likely limiting to forage growth when winter solar angles were

low and soil moisture was relatively accessible to growing forage (Figures 2–4, 8). Energy limitations on annual rangeland systems in California are recognized given that soil moisture conditions favorable to growth typically occur in winter and early spring when temperatures are not ideal for plant growth (Becchetti et al., 2016a; George et al., 1988). Temperature limitations in California rangeland have also been recognized by several regression modeling efforts that explained inter-annual forage variability as a function of site weather. Pitt and Hedy (1978) found positive associations between air temperature indices and standing forage in both March and June at the relatively wet HREC site. These indices aided in the power of their multiple regression models. Strong associations were found between counts of growing season degree days and standing forage at 11 range monitoring sites in California (R^2 from 0.75 to 0.95, George et al., 1988), in addition to associations with various seasonal precipitation totals and the lengths of midseason droughts (George et al., 1989). However, these reported positive associations between annual rangeland growth and temperature are in direct contradiction to a climate change manipulation study in the San Francisco Bay Area Jasper Ridge site that includes warming, CO₂ enrichment, and N fertilization, where no effects of an approximate 1°C warming were observed (Dukes et al., 2005; Zhu, Chiariello, Tobeck, Fukami, & Field, 2016). On the other hand, this is the same site where either negative or no association between warmer southern aspects and forage productivity was reported earlier (McNaughton, 1968).

4.2 | Aspect effect on soil moisture

It is generally accepted that aspect has an effect on microclimate and productivity in California rangelands with the expectation that south-facing terrain experiences more pronounced moisture limitations (Becchetti et al., 2016a; Eviner, 2016). However, despite the paucity of studies noted thirty years ago (Bartolome, 1989), there still remains a lack of studies describing and quantifying this relationship. The clearest aspect relationship to soil moisture occurred at the beginning of this study, initiated at the end of a historic and severe five-year drought (Figures 3, 4, 7). South-facing slopes were much drier throughout the 30-cm root zone, in spite of nearly 100 mm of precipitation that fell from mid-October through December 2016 (Figures S1, 3–4). Some of this early season discrepancy could have been enhanced by deep unsaturated flow to very dry soil below 15 cm on south-facing slopes, which may have dried to greater depths during the multi-year drought (Figures 3, 4). Alternatively, the drying may have been related to greater loss of new rainfall on warmer south-facing slopes (Figures 5, 6) through evaporation and plant transpiration. Low levels of plant cover and lack of residual dry matter in this early growth period would have favored evaporation over transpiration. Enhanced drying on south-facing slopes was also evident in late February 2017 and during the mid-winter drought of 2018 after germinating rains (Figures 3, 4, 7). Another study of the relationship between soil moisture and terrain features in the foothills of California similarly found that aspect explained 30%–50% of shallow volumetric soil moisture differences during

wet-up in a grassland catchment at SJER but not in an oak woodland at SFREC. Likewise, up to 80% of variability in springtime soil moisture dry-down was linked to aspect at the SJER grassland but not at SFREC where hydrostratigraphic complexity and more precipitation lead to a regular “fill and spill” phenomenon of water pooling above claypans and R horizons and spilling laterally downhill through the soil and above these layers (Beaudette et al., 2013; Swarowsky, Dahlgren, Tate, Hopmans, & O’Geen, 2011).

Heavy rains in January 2017 eliminated aspect-related soil moisture differences in the catchment and induced a 45-day period of deep percolation, showing that much of the precipitation in wet years is likely underutilized by annual forage species (Figures S1, 3, 4). Then, seven months of very little precipitation from June to December 2017 produced no aspect-related dry-down (Figures S1, 3, 4, 7). The relatively uniform dry-down is in line with the idea that soils will reach asymptotes of field drying at approximately half the wilting point of the soil (Allen, Pruitt, Raes, Smith, & Pereira, 2005). Less severe drying from 15–30 cm is also expected given that soil evaporation is provided mostly by the top 10–15 cm of soil along with some deep diffusive evaporation occurring at approximately 10%–15% of reference ET on bare soil (Figures 3, 4, Allen, Pereira, et al., 2005). Replenishment of soil water by upward capillary flow from deeply stored soil moisture originating in the wet year (2016–17) may also explain why soils did not dry down in a pattern related to aspect between growing seasons even though there were differences in warming (Figures 3–7). As noted above, a divergence in plant-available water related to aspect became apparent once rains returned in January 2018 but only at shallow depths where moisture penetrated and only after several weeks into the dry-down (Figures 3, 4, 7). Because there was not a dry-down pattern related to aspect before wetting, this divergence suggests that greater evaporative loss of recent rain on warmer, south-facing soils was the mechanism at work in both years’ wet-up phases. Ultimately, our study’s observation of aspect relationship to plant-available soil moisture levels in an annual grassland during wet-up phases shows that south-facing terrain in drier climates may be more susceptible to climate change impacts because precipitation whiplash (oscillations of drought with very wet years and mid-season dry periods) is expected to occur at a greater frequency in the future (Swain et al., 2018).

4.3 | Implications of a changing climate

There are several possible climate change implications for California annual range forage production related to this study’s findings. Given the past century of warming in California (Cordero, Kessomkiat, Abatzoglou, & Mauget, 2011) and a future of expected climate warming, California’s cold-limited annual range may become more productive during future wet years compared with historic wet years but mid-season droughts and species-specific responses may muddy this relationship. In a dry year, once ample rainfall occurred in late March and early April and soil moisture was easily accessible (Figures 3, 4), more rapid growth occurred on the warmer sites (Figure 9d), though at much lower rates of growth compared with a wet year

(Figure 10). Some recent efforts to forecast climate change impacts on California rangelands have overlooked temperature effects or midseason droughts on range production. For instance, a climate change impact study on California rangeland ecosystem services forecasted decreasing range productivity in the future but did not consider the possible positive effect of warming temperatures—only possible changes in precipitation patterns (Shaw et al., 2011). In contrast, a modeling study of climate change impacts on rangeland in the San Francisco Bay Area estimated that by the end of the 21st century, the region will produce 24%–40% more forage, but during seasons that are two weeks shorter (Chaplin-Kramer & George, 2013). However, the authors used a growing degree-day calculation for estimating future forage production that ignored the effects of mid-season droughts, which they acknowledged could alter their findings. A study that utilized an ecosystem process model called Biome-BGC found that southwestern US rangelands would likely experience declines in forage production but this region only included a portion of eastern and southeastern California, missing much of California's annual rangeland where winter growth is more important (Reeves et al., 2014). Two other syntheses of potential climate change impacts on US rangelands both surmised that southwestern and southern US rangelands will likely experience declines in productivity because of drier soils in a future of warming temperatures and lower precipitation (Polley et al., 2013; Reeves et al., 2017). Conclusions drawn from these nationwide modeling efforts may not translate well to Mediterranean annual rangeland, such as in California.

Moreover, large interannual swings in precipitation, as observed in this study and also typical of the regional climate (Figure S2; Dettinger, 2013), are expected to become even more pronounced with climate change (Swain et al., 2018). Variability in precipitation, a key driver of variability in forage production, makes optimal herd size selection a challenge. In the face of this unpredictability, improvements in seasonal precipitation forecasts could provide valuable information to ranch managers for drought risk management, as well as to optimize their operations to make use of abundant forage in wet years. However, reliable mid-to-long range precipitation forecasts remain elusive for California, as demonstrated recently by the unexpected winters of 2015–16 (continued drought) and 2016–17 (extreme precipitation). Enhancing seasonal weather forecast skill and future climate projection accuracy are an active area of research (Singh, Ting, Scaife, & Martin, 2018; Wang, Anichowski, Tippet, & Sobel, 2017) that should lead to improved capabilities to provide seasonal outlooks and longer term prediction of forage production.

While progress has been made to better understand possible climate change impacts on US rangelands, understanding will arguably be limited in regions with complex terrain until model resolution can match the scale of microclimate variability. Episodes of warming during extended midwinter drought could trigger sharp declines in forage, especially on warmer south-facing slopes, as observed in this study (Figure 9). But the relationship between standing forage and microclimate became distinctly nonlinear when soil moisture conditions improved. West- to northwest-facing sites were the most productive with greater forage growth than the coolest, north-facing

sites, where production did not recover after soil moisture conditions improved (Figures 3, 4, 9, S5). The partial recovery of south-facing slopes that experienced declines in standing forage during the mid-winter drought could partly be related to species composition differences (Figure S5). These locations were dominated by filaree, which is documented to be very tolerant of soil moisture stress (Busso, Fernandez, & Fedorenko, 1998; Cox & Conran, 1996). Ultimately, understanding of species level associations with different microclimates, such as detailed in several studies of California annual range species on different aspects (Evans et al., 1975; McNaughton, 1968; Raguse & Evans, 1977), in addition to finer model resolution, may be necessary for reliable climate change impact assessments.

5 | CONCLUSIONS

This study shows that the relationship between soil temperature and soil moisture (microclimate) is dynamic in complex terrain and both are related to patterns in catchment scale forage growth. However, the sign and strength of the associations between microclimate and forage growth were constantly shifting, with occasions of both positive and negative correlations with soil temperature and positive correlation with soil moisture. For example, we observed a wet winter when warmer landscape positions showed faster forage growth rates and then a midwinter drought in a dry year when forage growth ceased on the warmest sites; here, plant-available moisture had been completely exhausted. In general, approximately half of the variability in rapid, springtime forage growth in both years could be explained by microclimate that included an interaction between soil moisture and temperature. In one sense, this confirms past research that found interannual forage variability at long-term California range monitoring sites could be explained by interannual weather variability (Duncan & Woodmansee, 1975; George et al., 1988; George et al., 1989; Murphy, 1970; Pitt & Heady, 1978). Our finding of climate linkages to forage growth processes was at a different scale—the catchment—but variation at this scale was greater than the interannual variability in California range production reported at four multidecadal monitoring sites. High resolution ecosystem process models that take into account complex terrain features and microclimate are needed to better understand seasonal and multiyear drought implications for semiarid and arid ecosystems in the face of climate change. Projections of a warmer climate with more frequent precipitation extremes are of special concern to the south-facing slopes of Mediterranean rangelands, though all parts of Mediterranean rangeland landscapes may produce more forage in wet years of a warmer world.

DATA AVAILABILITY STATEMENT

The daily aggregated soil moisture (as both volumetric water content and fraction of plant-available water storage) and temperature data are available as supplementary materials. Raw fifteen-minute interval

data from the 2-year microclimate record are available from the corresponding author upon request. Forage productivity data and terrain characteristics at the sensor locations are available in supplementary Tables S1 and S2.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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